1964 T89

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1964

PROBLEMS OUTSTANDING IN THE EVOLUTION OF BRAIN FUNCTION

ROGER W. SPERRY
Hixon Professor of Psychobiology
California Institute of Technology
Pasadena, California

THE AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK : 1964

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN

Frederick Tilney, *The Brain in Relation to Behavior;* March 15, 1932
C. Judson Herrick, *Brains as Instruments of Biological Values;* April 6, 1933
D. M. S. Watson, *The Story of Fossil Brains from Fish to Man;* April 24, 1934
C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races;* April 25, 1935
Samuel T. Orton, *The Language Area of the Human Brain and Some of its Disorders;* May 15, 1936
R. W. Gerard, *Dynamic Neural Patterns;* April 15, 1937
Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and its Connection with the Transformation of the Skull;* May 5, 1938
G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates;* May 11, 1939
John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain;* May 2, 1940
Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates;* May 8, 1941
George Pinkley, *A History of the Human Brain;* May 14, 1942
James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin;* May 27, 1943
James Howard McGregor, *The Brain of Primates;* May 11, 1944
K. S. Lashley, *Neural Correlates of Intellect;* April 30, 1945
Warren S. McCulloch, *Finality and Form in Nervous Activity;* May 2, 1946
S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods;* May 8, 1947
Tilly Edinger, *The Evolution of the Brain;* May 20, 1948
Donald O. Hebb, *Evolution of Thought and Emotion;* April 20, 1949
Ward Campbell Halstead, *Brain and Intelligence;* April 26, 1950
Harry F. Harlow, *The Brain and Learned Behavior;* May 10, 1951
Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex;* May 7, 1952
Alfred S. Romer, *Brain Evolution in the Light of Vertebrate History;* May 21, 1953
Horace W. Magoun, *Regulatory Functions of the Brain Stem;* May 5, 1954
Fred A. Mettler, *Culture and the Structural Evolution of the Neural System;* April 21, 1955
Pinckney J. Harman, *Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny;* April 26, 1956
Davenport Hooker, *Evidence of Prenatal Function of the Central Nervous System in Man;* April 25, 1957
David P. C. Lloyd, *The Discrete and the Diffuse in Nervous Action;* May 8, 1958
Charles R. Noback, *The Heritage of the Human Brain;* May 6, 1959
Ernst Scharrer, *Brain Function and the Evolution of Cerebral Vascularization;* May 26, 1960
Paul I. Yakovlev, *Brain, Body and Behavior. Stereodynamic Organization of the Brain and of the Motility-Experience in Man Envisaged as a Biological Action System;* May 16, 1961
H. K. Hartline, *Principles of Neural Interaction in the Retina;* May 29, 1962
Harry Grundfest, *Specialization and Evolution of Bioelectric Activity;* May 28, 1963
Roger W. Sperry, *Problems Outstanding in the Evolution of Brain Function;* June 3, 1964

PROBLEMS OUTSTANDING IN THE EVOLUTION OF BRAIN FUNCTION

Having been for some time one of those "card-carrying members" of the American Museum and being indebted to the Museum on certain other counts over the years, I much appreciate the invitation to give the 1964 James Arthur Lecture. I have been forewarned that many in the audience will not be particularly carried away by the "latest technical advances." I have also been forewarned that another 50 per cent are apt to be rather bored by anything else. The motley mixture of material with which I have tried to balance the diverse interests will, I fear, strain even so broad an encompassing theme as that of evolution. As indicated in the title, we shall be concerned more with the functional than with the morphological properties of the brain, and more with remaining unsolved problems than with the solid progress over which we already can beat our chests.

I wish to skip the beginning steps in the evolution of the human brain and pick up the story at about the culmination of the latter half of the age of hydrogen gas. In such a way we can bypass what is by far the most difficult of all the unsolved problems in brain evolution, namely, how, when, and where did the hydrogen age and the whole business start? This problem we can leave to the proponents of the "steady state," the "periodic pulsation," and the "big bang," at least until someone comes along with a more credible interpretation of the meaning of the red shift.

We can skip quickly also through those early periods when, first, electrons and protons were being used to build bigger and better atoms, and then the atoms to make bigger and finer molecules, and then these in turn were being compounded into giant and replicating molecules and self-

organizing molecular complexes and eventually that elaborate unit, the living cell.

We need pause here only to note for future reference that evolution keeps complicating the universe by adding new phenomena that have new properties and new forces and that are regulated by new scientific principles and new scientific laws—all for future scientists in their respective disciplines to discover and formulate. Note also that the old simple laws and primeval forces of the hydrogen age never get lost or cancelled in the process of compounding the compounds. They do, however, get superseded, overwhelmed, and outclassed by the higher-level forces as these successively appear at the atomic, the molecular, and the cellular and higher levels.

We can turn now to what is probably the "most unanswered" problem in brain evolution. We encounter it a bit later on, presumably after organisms with nerve nets and brains have entered the picture. I refer, as you probably guess, to the first appearance of that most important of all brain properties and certainly the most precious, conscious awareness. (I hope that it is safe to assume that, since "mind" and "consciousness" have made a comeback in recent years and have become respectable terms again in the Boston area, it is permissible to mention them here also.)

In any case, the fossil record notwithstanding, there seems to be good reason to regard the evolutionary debut of consciousness as very possibly the most critical step in the whole of evolution. Before this, the entire cosmic process, we are told, was only, as someone has phrased it, "a play before empty benches"—colorless and silent at that, because, according to our best physics, before brains there was no color and no sound in the universe, nor was there any flavor or aroma and probably rather little sense and no feeling or emotion.

All of these can now be generated by the surgeon's elec-

trode tip applied to the proper region of the exposed conscious brain. They can be triggered also, of course, by the proper external stimuli, but also, more interestingly, by centrally initiated dream states, illusionogenic and hallucinogenic agents, but always and only within and by a brain. There probably is no more important quest in all science than the attempt to understand those very particular events in evolution by which brains worked out that special trick that has enabled them to add to the cosmic scheme of things: color, sound, pain, pleasure, and all the other facets of mental experience.

In searching brains for clues to the critical features that might be responsible, I have never myself been inclined to focus on the electrons, protons, or neutrons of the brain, or on its atoms. And, with all due respect to biochemistry and the N.R.P., I have not been inclined to look particularly at the little molecules of the brain or even at its big macromolecules in this connection. It has always seemed rather improbable that even a whole brain cell has what it takes to sense, to perceive, to feel, or to think on its own. The "search for psyche," in our own case at least, has been directed mainly at higher-level configurations of the brain, such as specialized circuit systems, and not just any juicy central nerve network that happens to be complex and teeming with electrical excitations. I have been inclined to look rather at circuits specifically designed for the express job of producing effects like pain, or High C or blue-yellow —circuits of the kind that one finds above a high transection of the spinal cord but not below, circuits with something that may well be present in the tiny pinhead dimensions of the midbrain of the color-perceiving goldfish but lacking in the massive spinal-cord tissue of the ox, circuits that are profoundly affected by certain lesions of the midbrain and thalamus but little altered by complete absence of the entire human cerebellum. Were it actually to come to laying our

money on the line, I should probably bet, first choice, on still larger cerebral configurations, configurations that include the combined effect of both (a) the specialized circuit systems such as the foregoing plus (b) a background of cerebral activity of the alert, waking type. Take away either the specific circuit, or the background, or the orderly activity from either one, and the conscious effect is gone.

In this day of information explosion, these matters are not so much of the "ivory tower" as they used to be: To the engineer who comes around from Industrial Associates with dollars and cents in his eye and company competition in his heart the possibility is of more than theoretical interest that conscious awareness may be something that is not necessarily tied to living hardware, that it could prove to be an emergent, over-all circuit property that might, in theory, be borrowed and, given sufficient acreage, perhaps copied some day in order to incorporate pain and pleasure, sensations and percepts, into the rapidly evolving circuitry of computer intellect. When the aim is to build into your circuit systems some kind of negative and positive reinforcement, then pain and pleasure are about the best kind. And eager young theoreticians from the NASA committee or from radio astronomy already want a more educated guess about the possibility of encountering on other globes other minds with perhaps totally different dimensions of conscious awareness, and if not, why not? Then there are more imminent, practical matters such as the need, in view of certain other explosions we face, to be able to pinpoint the first appearance of consciousness in embryonic development and chart its subsequent growth and maturation.

Unless you are among those who still believe that value judgments lie outside the realm of science, you may probably agree that a few reliable answers in these general areas and their implications could shake considerably the going value systems of our whole culture.

We shift now to certain lesser and subsidiary problems, but problems more approachable in research. Unlike the situation 25 years ago, most of us today are quite ready to talk about the evolution and inheritance not only of brain morphology but also of brain function, including general behavior and specific behavior traits. Earlier renunciation of the whole instinct concept in the animal kingdom generally stemmed in large part from our inability to imagine any growth mechanisms sufficiently precise and elaborate even to begin the fabrication of the complex nerve networks of behavior. This outlook was supported in the analytic studies of nerve growth all through the 1920's and 1930's which indicated that nerve fibers grow and connect in a random, diffuse, and non-selective manner governed almost entirely by indifferent, mechanical factors.

Today the situation is entirely changed. The supposed limitations in the machinery of nerve growth are largely removed in the new insight that we have obtained in recent years into the way in which the complicated nerve-fiber circuits of the brain grow, assemble, and organize themselves in a most detailed fashion through the use of intricate chemical codes under genetic control (Sperry, 1950a, 1950b, 1951, 1958, 1961, 1962, 1963). The new outlook holds that the cells of the brain are labeled early in development with individual identification tags, chemical in nature, whereby the billions of brain cells can thereafter be recognized and distinguished, one from another. These chemical differentials are extended into the fibers of the maturing brain cells as these begin to grow outward, in some cases over rather long distances, to lay down the complicated central communication lines. It appears from our latest evidence that the growing fibers select and follow specific prescribed pathways, all well marked by chemical guideposts that direct the fiber tips to their proper connection sites. After reaching their correct synaptic zones, the fibers then

link up selectively among the local population with only those neurons to which they find themselves specifically attracted and constitutionally matched by inherent chemical affinities.

The current scheme now gives us a general working picture of how it is possible, in principle at least, for behavioral nerve nets of the most complex and precise sorts to be built into the brain in advance without benefit of experience. Being under genetic control, these growth mechanisms are of course inheritable and subject to evolutionary development. The same is true of the differential endogenous physiological properties of the individual cell units in these networks which, along with the morphological interconnections, are of critical importance in the shaping of behavior patterns. We have at present only the general outlines and general principles of the developmental picture; much of the detail has yet to be worked out. Also, the underlying chemistry of the demonstrated selectivity in nerve growth, as well as the molecular basis of the morphogenetic gradients involved, and of all the rest of the chemical "I. D. Card" concept remains a wide-open field that so far has been virtually untouched.

In connection with this emphasis on the "inherited" in brain organization, one may well question the extent to which the observed inbuilt order in the anatomical structure necessarily conditions functional performance and behavior. Some years ago, when we subscribed to the doctrine of an almost omnipotent adaptation capacity in the central nervous system and to functional equipotentiality of cortical areas and to the functional interchangeability among nerve connections in general (Sperry, 1958), Karl Lashley surmised that if it were feasible, a surgical rotation through 180 degrees of the cortical brain center for vision would probably not much disturb visual perception. Rotation of the brain center was not feasible, but it was possible to

rotate the eyes surgically through 180 degrees in a number of the lower vertebrates and also to invert the eyeball, by transplantation from one to the other orbit, on the up-down or on the front-back axis and also to cross-connect the right and left eyes to the wrong side of the brain (Sperry, 1950a). All these and different combinations thereof were found to produce very profound disturbances of visual perception that were correlated directly in each case with the geometry of the sensory disarrangement. The animals, after recovery from the surgery, responded thereafter as if everything were to them upside down and backward, or reversed from left to right, and so on. Contrary to earlier suppositions regarding the dynamics of perception and cortical organization, it appeared that visual perception was very closely tied indeed to the underlying inherited structure of the neural machinery.

We inferred further from nerve-lesion experiments (Sperry, 1950b) on the illusory spinning effects produced by these visual inversions that the inbuilt machinery of perception must include also certain additional central mechanisms by which an animal is able to distinguish those sensory changes produced by its own movement from those originating outside. The perceptual constancy of an environment in which an animal is moving, for example, or of an environment that it is exploring by eye, head, or hand movements, would seem to require that, for every movement made, the brain must fire "corollary discharges" into the perceptual centers involved. These anticipate the displacement effect and act as a kind of correction or stabilizing factor. These centrally launched discharges must be differentially gauged for the direction, speed, and distance of each move. Along with the dynamic schema for body position which the brain must carry at all times, these postulated discharges conditioning perceptual expectancy at every move would appear to be a very important feature of the

unknown brain code for perception. The consistent appearance of the spontaneous optokinetic reaction of inverted vision in fishes, salamanders, and toads would indicate that the underlying mechanism is basic and must have evolved very early.

Since the representation of movement at higher cortical levels generally seems to be more in terms of the perceptual expectancy of the end effect of the movement than in terms of the actual motor patterns required to mediate the movement, the postulated "corollary discharges" of perceptual constancy may not involve so much of an additional load, in terms of data processing, as might at first appear.

We are ready now for that old question: How much of brain organization and behavior should we blame or credit to inheritance and how much to learning and experience? As far as we can see now, it seems fair to say that all that central nervous organization that is illustrated and described in the voluminous textbooks, treatises, and professional journals of neuro-anatomy, that is, all the species-constant patterning of brain structure, the micro-architecture as well as the gross morphology that has so far been demonstrated anatomically, seems to be attributable to inheritance. Another way of saying the same thing is that no one has yet succeeded in demonstrating anatomically a single fiber or fiber connection that could be said with assurance to have been implanted by learning. In this same connection, it is entirely conceivable (though not particularly indicated) that the remodeling effects left in the brain by learning and experience do not involve the addition or subtraction of any actual fibers or fiber connections but involve only physiological, perhaps membrane, changes that effect conductance or resistance to impulse transmission, or both, all within the existing ontogenetically determined networks.

The foregoing picture leaves plenty of room for learning and for the combined effects of learning plus maturation

during that prolonged period in human childhood when these two factors overlap. Nevertheless the present picture represents a very considerable shift of opinion over the past two decades in the direction of inheritance.

Some of you may find certain aspects here a bit difficult to reconcile with other inferences drawn in recent years from a series of sensory deprivation studies on mammals in which cats, monkeys, chimpanzees, and other animals have been raised in the dark or with translucent eye caps or in harnesses or holders of various sorts and in which, as a result of the various kinds of deprivation of experience in their early development the animals came to show subsequent deficits, moderate to severe, in their perceptual or motor capacities. The tendency to interpret these findings, along with those from human cataract cases, as evidence of the importance of early learning and experience in shaping the integrative organization of the brain we have long felt to have been overdone (Sperry, 1950a, 1962). In nearly all cases the findings could be equally well explained on the assumption that the effect of function is simply to maintain, or to prevent the loss of, neural organization already taken care of by growth. What the results have come to show in many of these studies is that certain of the newly formed neuronal elements, if abnormally deprived of adequate stimulation, undergo an atrophy of disuse. In much the same way cells of the skeletal muscles differentiate in development to the point at which they are contractile and ready to function, but then they too atrophy and degenerate if not activated. This basic developmental "use-dependent" property in maturing neurons, or even some evolutionary derivative of it, applied farther centrally beyond the sensory paths amid more diffuse growth pressures, especially among cortical association units, could, however, have true patterning effects and become a definitely positive factor in learning and imprinting.

We have been approaching very closely here the general problem of memory. Among brain functions, memory certainly rates as one of the prime "problems outstanding." Whatever the nature of the neural mechanism underlying memory, it seems to have appeared quite early in evolution. (Some writers say that even flatworms have memory!) We are frequently impressed in our own work with learning and memory in cats, and even in fishes, with the fact that their simple memories, once implanted, seem to be strong and lasting. With respect to memory, then, what separates the men from the animals is very likely not so much the nature of the neural trace mechanism as the volume and the kind of information handled. The problems that relate to the translation and coding of mental experience, first into the dynamics of the brain process, and then into the static, frozen, permanent trace or engram system, pose the more formidable aspects of the memory problem.

Fundamental to these memory questions, as also to the problems of perception, volition, learning, motivation, and most of the higher activities of the nervous system, is that big central unknown that most of us working on the higher properties of the brain keep tangling with and coming back to. You may find it referred to variously as: the "brain code," or the "cerebral correlates of mental experience," or the "unknown dynamics of cerebral organization," or the "intermediary language of the cerebral hemispheres," or, in some contexts, just the "black box." Thus far we lack even a reasonable hypothesis regarding the key variables in the brain events that correlate with even the simplest of mental activities, such as the elementary sensations or the simple volitional twitch of one's little finger.

In our own efforts to help to chip away at this central problem of the language of the hemispheres, we have been trying for some 10 years first to divide the problem in half by splitting the brain down the middle before we start to study

it. (Many times we wonder if the end effect of this split brain approach is not so much to halve our problems as it is to double them.) At any rate, the brain-bisection studies leave us with a strong suspicion that evolution may have saddled us all with a great deal of unnecessary duplication, both in structure and in the function of the higher brain centers.

Space in the intracranial regions is tight, and one wonders if this premium item could not have been utilized for better things than the kind of right-left duplication that now prevails. Evolution, of course, has made notable errors in the past, and one suspects that in the elaboration of the higher brain centers evolutionary progress is more encumbered than aided by the bilateralized scheme which, of course, is very deeply entrenched in the mechanisms of development and also in the basic wiring plan of the lower nerve centers.

Do we really need two brain centers, for example, to tell us that our blood sugar is down or our blood pressure is up, or that we are too hot or too cold, and so on? Is it necessary to have a right and also a left brain center to let us know that we are sleepy or angry, sad or exuberant, or that what we smell is Arpege or what we taste is salty or that what we hear is voices, and so on and on and on? Surely most of us could manage to get along very well with only one cerebral anxiety mechanism, preferably in the minor hemisphere.

Emotion, personality, intellect, and language, among other brain business, would seem by nature to be quite manageable through a single unified set of brain controls. Indeed, the early loss of one entire hemisphere in the cat, monkey, and even in man causes amazingly little deficit in the higher cerebral activities in general.

With the existing cerebral system, most memories as well have to be laid down twice—one engram for the left

hemisphere and another engram copy for the right hemisphere. The amount of information stored in memory in a mammalian brain is a remarkable thing in itself; to have to double it all for the second hemisphere would seem in many ways a bit wasteful. It is doubtful that all this redundancy has had any direct survival value (unless evolution could have foreseen that neurologists would be opening and closing the cranium to produce brain lesions under careful aseptic conditions that permit survival).

In the human brain, of course, we begin to see definite evidence of a belated tendency in evolution to try to circumvent some of the duplication difficulties. A de-duplication trend is seen particularly in the lateralization of speech and writing within the single dominant hemisphere in the majority of persons. Speech, incidentally, is another essentially symmetrical activity for which a double right and left control is quite unnecessary, even at the lower levels of the motor hierarchy. When the brain does try in some individuals to set up two central administrations for speech, one in each hemisphere, the result tends to make for trouble, like stammering and a variety of other language difficulties.

The fact that the corpus callosum interconnecting the two cerebral hemispheres is so very large and the functional damage produced by its surgical section is so very minor in most ordinary activities seems to be explainable in part by the fact that the great cerebral commissure is a system for cross communication between two entities that to a large extent are each completely equipped and functionally self-sufficient. The corpus callosum appears late in evolution, being essentially a mammalian structure, and its development is closely correlated with the evolutionary elaboration of the neocortex of the mammalian cerebral hemispheres.

Accordingly it is not surprising that it is in the human

brain, and particularly in connection with speech, that the functional effects produced by surgical disconnection of the two cerebral hemispheres become most conspicuous. During the past two years we have had an opportunity to test and to study two patients, formerly unmanageable epileptics, who have had their right and left hemispheres disconnected by complete section of the corpus callosum, plus the anterior commissure, plus the hippocampal commissure, plus the massa intermedia, in what is perhaps the most radical surgical approach to epilepsy thus far undertaken. The surgery was done by Drs. Philip J. Vogel and Joseph E. Bogen (see Bogen and Vogel, 1962) of Los Angeles.[1]

It seemed a reasonable hope, in advance, that such surgery might help to restrict the seizures to one hemisphere and hence to one side of the body, and possibly to the distal portions of arm and leg, since voluntary control of both sides of the head, neck, and trunk tends to be represented in both hemispheres. In our colony of split-brain monkeys that have had similar surgery, we not uncommonly see epileptic-like seizures, especially during the early weeks after brain operations, and these seizures show a definite tendency to center in the distal extremities of the arm and leg and to be restricted to one side. It also seemed reasonable that this surgery might help the patients to retain consciousness in one hemisphere during an attack, if not throughout, at least during the early stages, and thereby give them a chance to do things that might help to break

[1]The surgical treatment of these cases was undertaken at the suggestion of Dr. Bogen after extensive consultations on all aspects. The surgery was performed by Dr. Vogel, assisted by Dr. Bogen and other staff members at the Loma Linda Neurosurgical Unit, White Memorial Hospital. Most of the tests reported here were planned and administered by Michael S. Gazzaniga of our laboratory, with the writer collaborating on a general advisory basis.

The original work included here was supported by grants from the National Institutes of Health (MH-03372, S-F1-MH-18,080) and by the Frank P. Hixon Fund of the California Institute of Technology.

or control the seizures, or at a minimum to allow time in which to undertake protective measures before the second side became involved. It was further hoped that such surgery might reduce the severity of the attacks by the elimination of a very powerful avenue for the right-left mutual reinforcement of the seizures during the generalized phase, especially during *status epilepticus,* which was of major concern in both the cases cited above.

Judged from earlier reports of the cutting of the corpus callosum and from the behavior of dozens of monkeys that we have observed in the laboratory with exactly the same surgery (Sperry, 1961, 1964), it seemed unlikely that this kind of surgery would produce any severe handicap, or surely none so bad as certain other forms of psychosurgery that have been used on a much more extensive scale. That the surgery might decrease the incidence of the seizures to the point of virtually eliminating them (as it seems to have done so far in both cases) was unexpected; our fingers remain very much crossed on this latter point.

Everything that we have seen so far indicates that the surgery has left each of these people with two separate minds, i.e., with two separate spheres of consciousness (Gazzaniga, Bogen, and Sperry, 1962, 1963). What is experienced in the right hemisphere seems to be entirely outside the realm of awareness of the left hemisphere. This mental duplicity has been demonstrated in regard to perception, cognition, learning, and memory. One of the hemispheres, the left, dominant, or major hemisphere, has speech and is normally talkative and conversant. The other mind of the minor hemisphere, however, is mute or dumb, being able to express itself only through non-verbal reactions; hence mental duplicity in these people following the surgery, but no double talk.

Fortunately, from the patients' standpoint, the functional separation of the two hemispheres is counteracted by a large

number of unifying factors that tend to keep the disconnected hemispheres doing very much the same thing from one part of the day to the next. Ordinarily, a large common denominator of similar activity is going in each. When we deliberately induce different activities in right and left hemispheres in our testing procedures, however, it then appears that each hemisphere is quite oblivious to the experiences of the other, regardless of whether the going activities match or not.

This is illustrated in many ways: For example, the subject may be blindfolded, and a familiar object such as a pencil, a cigaret, a comb, or a coin is placed in the left hand. Under these conditions, the mute hemisphere connected to the left hand, feeling the object, perceives and appears to know quite well what the object is. It can manipulate it correctly; it can demonstrate how the object is supposed to be used; and it can remember the object and go out and retrieve it with the same hand from among an array of other objects. While all this is going on, the other hemisphere has no conception of what the object is and says so. If pressed for an answer, the speech hemisphere can only resort to the wildest of guesses. So the situation remains just so long as the blindfold is kept in place and other avenues of sensory input from the object to the talking hemisphere are blocked. But let the right hand cross over and touch the test object in the left hand; or let the object itself touch the face or head as in the use of a comb, a cigaret, or glasses; or let the object make some give-away sound, such as the jingle of a key case, then immediately the speech hemisphere produces the correct answer.

The same kind of right-left mental separation is seen in tests involving vision. Recall that the right half of the visual field and the right hand are represented together in the left hemisphere and vice versa. Visual stimuli such as pictures, words, numbers, and geometric forms flashed on a

screen directly in front of the subject and to the right side of a central fixation point are all described and reported correctly with no special difficulty. On the other hand similar material flashed to the left half of the visual field is completely lost to the talking hemisphere. Stimuli flashed to one half field seem to have no influence whatever, in tests to date, on the perception and interpretation of stimuli presented to the other half field.

Note in passing that these disconnection effects do not show up readily in ordinary behavior. They must be demonstrated by the flashing of the visual material fast enough so that eye movements cannot be used to sneak the answers into the wrong hemisphere, or in the testing of right and left hands vision must be excluded with a blindfold, auditory cues eliminated, and the hands kept from crossing, and so on. One of the patients, a 30-year old housewife with two children, goes to market, runs the house, cooks the meals, watches television, and goes out to complete, three-hour shows at the drive-in theater, all without complaining of any particular splitting or doubling in her perceptual experience. Her family believes that she still does not have so much initiative as formerly in her housecleaning, in which she was meticulous, and that her orientation is not so good, for example, she does not find her way back to the car at the drive-in theater as readily as she formerly could. In the early months after surgery there appeared to be definite difficulty with memory. By now, some eight months later, there seems to be much improvement in this regard, though not complete recovery. Involvement of the fornix would have to be ruled out before effects like the latter can be ascribed to the commissurotomy.

In the visual tests again, one finds plenty of evidence that the minor, dumb, or mute hemisphere really does perceive and comprehend, even though it cannot express verbally what it sees and thinks. It can point out with the left hand

a matching picture from among many others that have been flashed to the left field, or it can point to a corresponding object that was pictured in the left-field screen. It can also pick out the correct written name of an object that it has seen flashed on the screen, or vice versa. In other words, Gazzaniga's more recent results show that the dumb left hemisphere in the second patient is not exactly stupid or illiterate; it reads a word such as "cup," "fork," or "apple" flashed to the left field and then picks out the corresponding object with the left hand. While the left hand and its hemisphere are thus performing correctly, however, the other hemisphere, again, has no idea at all which object or which picture or which name is the correct one and makes this clear through its verbal as well as other responses. You regularly have to convince the talking hemisphere to keep quiet and to let the left hand go ahead on its own, in which case it will usually pick out the correct answer.

These minor differences of opinion between the right and left hemispheres are seen rather commonly in testing situations. For example, the left hand is allowed to feel and to manipulate, say, a toothbrush under the table or out of sight behind a screen. Then a series of five to 10 cards are laid out with names on them such as "ring," "key," "fork." When asked, the subject may tell you that what she felt in the left hand was a "ring." However, when instructed to point with the left hand, the speechless hemisphere deliberately ignores the erroneous opinions of its better half and goes ahead independently to point out the correct answer, in this case the card with the word "toothbrush."

As far as we can see, about the only avenue remaining for direct communication between mind-right and mind-left is that of extrasensory perception. If any two minds should be able to tune in on each other, one might expect these two to be able to do so, but thus far no evidence of such effects is apparent in the test performances.

The conscious awareness of the minor hemisphere produced by this vertical splitting of the brain often seems so remote to the conversant hemisphere as to be comparable perhaps to that produced by a spinal transection. To go back here to some of the issues on which we started, one wonders if we can really rule out, as I implied above, the alternative contention of those who maintain that spinal cords, loaves of bread, and even single molecules have a kind of consciousness. Either way, the inferences to be drawn regarding the evolution and elaboration of consciousness for most practical purposes remain much the same.

We are often asked if each of the disconnected hemispheres must not also have a will of its own and if the two do not then get into conflict with each other. In the first half year after surgery, particularly with the first patient, we got reports suggesting something of the kind. For example, while the patient was dressing and trying to pull on his trousers, the left hand started to work against the right, pulling them off again. Or, the left hand, after just helping to tie the belt of his robe, went ahead on its own to untie the completed knot, whereupon the right hand would have to supervene again to get it retied. The patient and his wife used to refer to the "sinister left hand" which sometimes tried to push the wife away aggressively at the same time that the hemisphere of the right hand was trying to get her to come and help him with something. These antagonistic movements of right and left hands are fairly well restricted to situations in which the reactions of left and right hand are easily made from the same common supporting posture of body and shoulders. Generally speaking, there are so many unifying factors in the situation and functional harmony is so strongly built into the undivided brain stem and spinal networks, by express design, that one sees little overt expression or overflow into action, at least, of conflicting will power.

This matter of having two free wills packed together inside the same cranial vault reminds us that, after consciousness, free will is probably the next most treasured property of the human brain. Questions and information relating to the evolution of free will have practical impact rating right at the top, along with those of consciousness. As such it probably deserves at least a closing comment. Some maintain that free will is an evolved, emergent property of the brain that appeared between man and the higher apes, or, depending on whom you read, maybe somewhere after bacteria perhaps, but before houseflies.

Unlike "mind," "consciousness," and "instinct," "free will" has made no comeback in behavioral science in recent years. Most behavioral scientists would refuse to list free will among our problems outstanding, or at least as an unanswered problem. (To agree that behavior is unlawful in this respect might put them out of work as scientists, you see, and oblige them perhaps to sign up with the astrologers' union.) Every advance in the science of behavior, whether it has come from the psychiatrist's couch, from microelectrode recording, from brain-splitting, or from the running of cannibalistic flatworms, seems only to reinforce that old suspicion that free will is just an illusion. The more we learn about the brain and behavior, the more deterministic, lawful, and causal it appears.

In other words, behavioral science tells us that there is no reason to think that any of us here tonight had any real choice to be anywhere else, or even to believe in principle that our presence here was not already "in the cards," so to speak, five, 10, or 15 years ago. I do not feel comfortable with this kind of thinking any more than you do, but so far I have not found any satisfactory way around it. Alternatives to the rule of causal determinism in behavior proposed so far, like the inferred unlawfulness in the dance of subatomic particles, seem decidedly more to be deplored as a solution

than desired.

The above statements are not to say that, in the practice of behavioral sciences, we must regard the brain as just a pawn of the physical and chemical forces that play in and around it. Far from it. To go back to the beginning of the present lecture, recall that a molecule in many respects is the master of its inner atoms and electrons. The latter are hauled and forced about in chemical interactions by the over-all configurational properties of the whole molecule. At the same time, if our given molecule is itself part of a single-celled organism such as paramecium, it in turn is obliged, with all its parts and its partners, to follow along a trail of events in time and space determined largely by the extrinsic over-all dynamics of *Paramecium caudatum*. When it comes to brains, remember that the simpler electric, atomic, molecular, and cellular forces and laws, though still present and operating, have been superseded by the configurational forces of higher-level mechanisms. At the top, in the human brain, these include the powers of perception, cognition, reason, judgment, and the like, the operational, causal effects and forces of which are equally or more potent in brain dynamics than are the outclassed inner chemical forces.

You sense the underlying policy here: "If you can't lick 'em, join 'em," or, as Confucius might say, "If fate inevitable, relax and enjoy," or, "There may be worse fates than causal determinism." Maybe, after all, it is better to be embedded firmly in the causal flow of cosmic forces, as an integral part thereof, than to be on the loose and out of contact with these forces, "free floating" as it were and with behavioral possibilities that have no antecedent cause and hence no reason, nor any reliability when it comes to future plans, predictions, or promises.

And on this same theme, just one final point: If you were assigned the task of trying to design and build the perfect

free-will model (let us say the perfect, all-wise, decision-making machine to top all competitors' decision-making machines), consider the possibility that your aim might not be so much to free the machinery from causal contact, as the opposite, that is, to try to incorporate into your model the potential value of universal causal contact; in other words, contact with all related information in proper proportion—past, present, and future.

It is clear that the human brain has come a long way in evolution in exactly this direction when you consider the amount and the kind of causal factors that this multidimensional intracranial vortex draws into itself, scans, and brings to bear on the process of turning out one of its "preordained decisions." Potentially included, thanks to memory, are the events and collected wisdom of most of a human lifetime. We can also include, given a trip to the library, the accumulated knowledge of all recorded history. And we must add to all the foregoing, thanks to reason and logic, much of the future forecast and predictive value extractable from all these data. Maybe the total falls a bit short of universal causal contact; maybe it is not even quite up to the kind of thing that evolution has going for itself over on Galaxy Nine; and maybe, in spite of all, any decision that comes out is still predetermined. Nevertheless it still represents a very long jump in the direction of freedom from the primeval slime mold, the Jurassic sand dollar, or even the latest 1964-model orangutan.

LITERATURE CITED

BOGEN, J. E., AND P. J. VOGEL

1962. Cerebral commissurotomy in man. Bull. Los Angeles Neurol. Soc., vol. 27, p. 169.

GAZZANIGA, M. S., J. E. BOGEN, AND R. W. SPERRY

1962. Some functional effects of sectioning the cerebral commissures in man.

Proc. Natl. Acad. Sci., vol. 48, pt. 2, p. 1765.

1963. Laterality effects in somesthesis following cerebral commissurotomy in man. Neuropsychologia, vol. 1, p. 209.

SPERRY, R. W.

1950a. Mechanisms of neural maturation. *In* Stevens, S. S. (ed.), Handbook of experimental psychology. New York, John Wiley and Sons, p. 236.

1950b. Neural basis of the spontaneous optokinetic response produced by visual inversion. Jour. Comp. Physchol., vol. 43, p. 482.

1951. Regulative factors in the orderly growth of neural circuits. Growth Symp., vol. 10, p. 63.

1958. Physiological plasticity and brain circuit theory. *In* Harlow, H. F., and C. N. Woolsey (eds.), Biological and biochemical bases of behavior. Madison, University of Wisconsin Press.

1961. Some developments in brain lesion studies of learning. Fed. Proc., vol. 20, p. 609.

1962. How a random array of cells can learn to tell whether a straight line is straight—discussion on. *In* Foerster, H. von, and G. W. Zopf, Jr. (eds.), Principles of self-organization. New York, Pergamon Press, p. 323.

1963. Chemoaffinity in the orderly growth of nerve fiber patterns and connections. Proc. Natl. Acad. Sci., vol. 50, p. 703.

1964. The great cerebral commissure. Sci. Amer., vol. 210, p. 42.